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EXPERIMENTAL EVIDENCE ON THE EFFECTIVENESS OF SELECTION[1]

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IN studying the problems of evolution in the common infusorian *Paramecium,* I found that by methodical and progressive selection striking results can be reached.

From a wild culture it is possible by progressively selecting in two opposite directions to obtain finally two lots, one of which is many times as large as the other, and the differences between the two are permanent and hereditary. By properly regulated selection a great variety of permanently differentiated lots are obtainable.

Throughout this work Galton's law of regression was found to hold; that is, the progeny of extreme parents inherited the peculiarities of their parents, but in a less marked degree. Furthermore, the results were such as to lend themselves readily to interpretation as exemplifying Galton's law of ancestral heredity.

Thus the effectiveness of selection was clearly demonstrated. But just what sort of effectiveness does the theory that selection is the dynamic factor in evolution demand? It demands that selection shall so act that it might finally produce progress from *Amœba* up to man. It must produce, from a given condition, something that did not before exist in that given condition.

Has selection so acted in this case? To answer this question, we must evidently know precisely what exists in the condition with which we start. We therefore next work with the progeny of a single individual—forming a "pure line," the characteristics of which we thoroughly know.

Now we try the effects of selection on this pure line.

[1] A paper read before the American Society of Naturalists, December 29, 1909.

Not the faintest trace of effect is produced, even by long-continued methodical selection for hundreds of generations. The race or line is absolutely permanent, so far as the appearance of any hereditary differences are concerned. The individuals of the line do indeed differ greatly among themselves, but these differences are not inherited; they furnish absolutely no foothold for selection.

Examination showed that *Paramecium* consists of many such races, differing among themselves slightly, but each race as unyielding as iron. And the extreme races found in the wild culture are precisely the extremes obtainable by long-continued selection.

The effects of selection have then consisted simply and solely in isolating races that already existed. It had produced nothing new; there had been no progress that would form a step, however slight, in the journey from *Amœba* to man.

When I had reached this point I looked about and found that others had been having similar experiences. The investigator who discovers these things for himself finds perhaps that

> Es ist eine alte Geschichte
> Doch bleibt sie immer neu.

And the second line is as true as the first, for to one who has put months and years on such attempts to accomplish results by methodical selection, its utter powerlessness comes with new and surprising force. Johannsen in working with beans and barley, Hanel with *Hydra,* had found many pure lines existing in nature, but as in my own case, each pure line was absolutely unyielding.

But we know that others *had* found selection effective; a whole series of cases comes at once to our lips. Galton in studying peas and men; Fritz Müller with maize; de Vries with maize and with buttercups, MacCurdy and Castle with guinea pigs and rats—all these had reported definite progress as a result of methodical selection.

Why this difference? Is there one law for the Jews, another for the Gentiles?

Looking into the matter with care, we find that the results with our own material are, after all, like those of the investigators mentioned if we treat it in the same way. None of these workers first isolated their pure races. If we begin with a mixture we can, in beans, in barley, in *Paramecium,* in *Hydra,* by a methodical process of slow selection make gradual progress in a certain direction. But our selection is only a process of purification, and when we finally get a pure race, selection is utterly powerless to go farther. We should have been completely in the dark as to the real effect of selection if we had not carried through rigidly the "pure line" idea.

Is it possible then that we have in this pure line idea an instrument of the greatest importance for analysis? Is it perhaps the key which every one must have in order to understand the results of selection? May it be indeed one of those fundamental ideas which, like the idea of mutation, is fitted to clear and crystallize a confused and turbid mixture? Is it possibly of sufficient importance to deserve agitating a little before the American Society of Naturalists?

Let us put these questions to the practical test; let us apply the idea as an instrument for the dissection of the classic cases which seem to demonstrate the efficacy of selection in producing change of type.

Johannsen in his recent book has used the pure line concept as an instrument for analysis of the entire field of variation, heredity and evolution, and to him is due the credit of first perceiving the importance of this concept, when sharply defined, as such an instrument for research and presentation. The work of Johannsen, I believe, will remain one of the landmarks of progress in this field. But my own analysis has been independent of Johannsen's and diverse from it, developing inevitably from what I have myself seen, so that I may venture still to present some of its results.

But how can we apply the pure line idea to organisms whose lines are *not* pure; organisms that interbreed freely; organisms in which the characters of a given line split off, separate, and become exchanged for those of other lines, in the way characteristic of Mendelian inheritance?

The pure line idea here becomes a little elusive, a little abstract. But possibly it is still helpful as an instrument of analysis; let us try it. In order not to emphasize purity where impurity is the rule, let us substitute Johannsen's term *genotype* for "pure line"—defining the genotype as a set of individuals which, so long as they are interbred, produce progeny that are characteristically uniform in their hereditary features, not systematically splitting into diverse groups.

Now, how can we determine whether the genotype concept, with its consequences for the effects of selection, applies to organisms with biparental inheritance? Reflection shows that if it does, certain general propositions are true: if these propositions are found to hold, the genotypic explanation of the effects of selection is confirmed.

1. The first proposition is this: Organisms in which selection has shown itself effective are composed of many genotypes; of many races that are diverse in their hereditary characters. This we know to be true.

2. Second, from such a mixture of genotypes it is possible to isolate by selection any of the things that are present—perhaps in a great number of different combinations.

3. But from such a mixture it is *not* possible to get by methodical selection anything not present (save when rare mutations have occurred).

4. Therefore it is not possible to get by methodical selection anything lying outside the extremes of the genotypic characters already existing.

This is perhaps practically our most important proposition. For in order that selection shall produce pro-

gression from *Amœba* to man, it is evidently necessary that it should give us characters lying beyond the extremes of what already exists.

5. Our fifth proposition is that in the case of genotypes that cross-breed readily, we may get an indefinite number of combinations of all that lies between the extremes of the existing genotypes—the variety of combinations realized depending on the rules of inheritance.

Now, if we test by these propositions the classic cases of effective selection, what is the result?

Galton's work with peas and with men yields at once to the analysis, giving precisely the results which the genotypic idea requires. A by-product of the analysis is the practical evaporation of the laws of regression and of ancestral inheritance so far as their supposed physiological significance is concerned;[2] they are found to be the product mainly of a lack of distinction between two absolutely diverse things—between non-heritable fluctuations on the one hand, and permanent genotypic differentiations on the other.

The experiments of Müller and de Vries on maize yield with equal readiness. In these cases the male parents are unknown; the freest sort of crossing was occurring, and what selection did was pick out the progeny of extreme male genotypes, till the result approached the limit of the most extreme existing genotype under the cultural conditions.

MacCurdy and Castle's experiments in changing by selection the color-patterns of rats and guinea-pigs dealt

[2] This significance was supposed to lie in showing that the characteristics of the progeny depend upon the characteristics of the ancestors for many generations back, in ways that are definable. "Mr. Galton's view of the effect of regression follows inevitably from the general theory of chance, if we regard the character of an individual as a phenomenon due to a series of complex groups of causes, *among which are the characters of each ancestor.*" (W. F. R. Weldon, *Biometrika*, I, p. 370.)

The law of ancestral inheritance does not hold in pure lines, even in a statistical sense, as has repeatedly been shown. The progress of a long series of extreme ancestors does not differ from those of a series of average ancestors.

with races of complicated descent; they plunge us at once into all the difficulties due to interweaving, blending and transfer of characters from one genotype to another. But if we stick closely to the general propositions already stated, we shall have a guide. MacCurdy and Castle got by selection all sorts of conditions lying between the extremes with which they started. But did they get anything lying outside these extremes, as would be required in order to show that we can by selection make evolutionary progress? As I read their results, they did *not*. Their experiments are most important for many problems of variation and inheritance, but they do not give us evidence that methodical selection can produce anything beyond combinations of what already exists; hence they do not help us in getting from *Amœba* to man.

The work of the German breeders who have for years practised methodical selection for improvement of agricultural races clears up at once under the genotype idea, as the analyses of Fruwirth, v. Rümker and others show us. Continued methodical selection is often necessary, but what it does is to purify a contaminated race—a process which, owing to the laws of inheritance, may require several generations.

I have spoken only of those experiments which seem at first view to show the efficacy of selection; brevity requires me to pass without mention over investigations which, while not carried on with pure lines, support and reinforce the conclusions drawn from such work. Such for example are the fundamental experiments of Tower, the recent work of Pearl, of Shull, and many of the experiments of de Vries.

Thus far the dissecting knife of the pure line idea succeeds admirably in letting the light into the obscure workings of selection. Any one who uses it with precision will find what an important advance its exact formulation by Johannsen marks over even such an analysis as that given by de Vries. In the work of de Vries, as in that of many recent authors, the selection

idea is appraised at essentially its true value, but much in its action is left obscure. The reader is surprised at the accounts of experiments in which selection does accomplish marked results, though according to the general theory, it should not; one is left puzzled in judgment as to what we may expect from it. With the sharply formulated pure line concept as a guide, most of this obscurity disappears.

And then, to keep us from resting on our oars; to give us humility and spur us to further work—we come to the one case in which the pure line idea fails to bring clearness. This is de Vries's experiment with buttercups. Here, after selection the extreme was moved far beyond that before selection. Before selection the extreme number of petals was eleven; after selection it was thirty-one. Before selection no single individual had an average number of petals above six; after selection the average of all was above nine, and some had an average of thirteen! It is true that there are "mitigating circumstances" here; the work was not done with pure lines, and the variations dealt with are not of the ordinary fluctuating sort (as de Vries points out); change in cultural conditions doubtless played also a large part. Possibly repetition with thorough analytical experimentation will show that something besides selection has brought about the great changes. But at present the case stands sharply against the generalizations from the pure line work. It is the only such case that I have found.

To sum up, one finds not only that his own results and those of many other modern workers give the pure line interpretation, but also that all other cases that had seemed to point the other way yield readily to the genotypic analysis—save one. If we ride rough shod over this case, as not yet sufficiently studied, then we may draw a tentative conclusion as follows:

The pure line or genotype idea is the one to see clearly and grasp firmly in experimental investigations on selection. Many even of the modern experiments remain

obscure in their significance simply because the workers have not grasped this concept, have not shown the relation of their results to it. Further, in presenting one's own work, or in interpreting the accounts of others, the genotype concept is the instrument of precision to take in hand. The results of the analysis made by its aid indicate that most or all of the experiments in methodical selection have consisted in shifting about, isolating and recombining preexisting, permanent hereditary differentiations, giving results that were interpreted as revealing the law of actually progressive evolution, though in reality they had no relation to such a law.

To our conclusion as to the analytical value of the pure line idea we may expect strenuous opposition on the part of that last small remnant (if there be such a remnant) of the biometrical school that still submits to the dictation of Pearson[3]—for by one of those sardonic paradoxes through which nature revenges herself, the men who from outside have lectured biology on the necessity of becoming exact are the strongest opponents of exact experimental and biological analysis—seeming to feel that mathematical treatment renders other kinds of exactness undesirable.[4] Those who find the genotype idea useful may then prepare themselves for one of those justly famous bludgeonings from the dictator of the whilom orthodox biometrical school; this is the last honorable mark of distinction which stamps the investigator as a thorough and exact analyst of things biological.[5]

[3] Note how quickly the biometricians that devote themselves to careful biological investigations fall away from the Pearsonian faith. Darbishire, Davenport, Tower, Shull, Johannsen, Pearl; are there any biologists of achievement that still hold with Pearson?

[4] Pearson in 1901 informs us that evolution is a field "where no tabulation of individual instances can possibly lead to definite conclusions" (*Biometrika*, I, p. 344). This was the year of the appearance of de Vries's *Mutationstheorie*, and of the revival of Mendelism. Compare in definiteness and value the conclusions drawn from the work inaugurated in these two lines, based as it was precisely on the "tabulation of individual instances," with those from the biometrical work, with its careful avoidance of "individual instances."

[5] To name the men who have been subjected to Pearson's most savage

A word more on certain general questions. Can we conclude that if selection has no dynamic effect in changing existing genotypes, that therefore it need not be reckoned with in evolution? Or must we conclude that if it is to be reckoned with at all, selection has opportunity to act only on large leaps in evolution; that evolution takes place by such leaps, and not by imperceptibly small changes?

Such evidence as the pure line work gives implies neither of these things. The differences between the diverse pure lines *have* arisen in some way, if evolution occurs, and once these differences have arisen, they are open to the operation of selection as are any other differences. What the pure line work shows (agreeing in this with other lines of evidence) is that the changes on which selection may act are few and far between, instead of abundant; that they are found not oftener than in one individual in ten thousand, instead of being exhibited on comparing any two specimens; that a large share of the differences between individuals are not of significance for selection or evolution—these being precisely the differences measured as a rule by the biometrician's "coefficient of variation." Thus the work of natural selection is made infinitely more difficult and slow; but logically it is still possible.

Nor does the pure line work assist natural selection, as some have hoped from the mutation work, by making the steps in evolution greater in amount. On the contrary, the work with genotypes brings out as never before the minuteness of the hereditary differences that separate the various lines. These differences are the smallest that can possibly be detected by refined measurements taken in connection with statistical treatment. Johannsen found his genotypes of beans differing constantly merely by weights of two or three hundredths of a gram in the average weight of the seed. Genotypes

assaults is to name the men that have done most to advance our knowledge of heredity. The cases of Castle and of Bateson will occur to every zoologist.

of *Paramecium* I found to show constant hereditary differences of one two-hundredth of a millimeter in length. Hanel found the genotypes of *Hydra* to differ in the average number of tentacles merely by the fraction of a tentacle. That even smaller hereditary differences are not described is certainly due only to the impossibility of more accurate measurements; the observed differences go straight down to the limits set by the probable error of our measures. Genotypes so differing have not risen from one another by large mutations. The genotypic work lends no support to the idea that evolution occurs by large steps, for it reveals a continuous series of the minutest differences between great numbers of existing races.

All together, I think we may say that the pure line or genotype concept presents an instrument of analysis which is worthy, on the basis of what it has thus far done, of a thorough tryout for future work, and no one interested in these questions can afford to neglect it. This conclusion is quite independent of the concrete results reached; the efficacy of selection in modifying genotypes may be demonstrated to-morrow, but the demonstrators will need to show precisely the relation of their results to the pure line concept.